



Zonal adaptation in pearl millet [*Pennisetum glaucum* (L.) R. Br.] cultivar types

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Abstract

The pearl millet [*Pennisetum glaucum* (L.) R. Br.] growing area of India is divided into three zones: the arid northwest (A1), the more favorable northern area (A) and the peninsular area (B), based on environmental factors. This study was done to assess adaptation patterns among common cultivar types to these three zones. Thirty cultivars (arid zone landraces, open-pollinated dual-purpose varieties and grain-type F_1 hybrids) were grown over two years in a representative location of each three main zones, plus an additional, severely drought stressed A1 zone location. The F_1 hybrids demonstrated a stable adaptation to all zones, in terms of both biomass and HI, although their actual level of biomass was the least of all three cultivar types. The landraces showed a strong specific adaptation to the A1 zone, in terms of both biomass and HI. The open-pollinated varieties, by contrast, were preferentially adapted to the A and B zones, and not to the A1 zone. The results are discussed in terms of the genetic origin of the various cultivar types and the implications for the genetic improvement of pearl millet on an All-India basis.

Key words: Pearl millet, adaptation, genotype \times environment interaction, cultivar type

Introduction

Pearl millet [*Pennisetum glaucum* (L.) R. Br.] is grown in India from 10° to 30° north latitude, from 200 mm to > 600 mm seasonal rainfall, on a wide range of soil types, and in a variety of both irrigated and rainfed production systems. The All-India Coordinated Pearl Millet Improvement Project (AICPMIP) has divided the pearl millet growing area of the country into three separate zones, recognizing that the requirements for adaptation differ significantly across the country. These zones have been designated as A1 (the arid zone of NW India), A (the higher rainfall areas of north and central India) and B (semi-arid peninsular India) [1].

Modern high yielding cultivars (mainly grain type F_1 hybrids, bred in the A and B zones) have been widely adopted by farmers in most of the A and B zones, but not in the A1 zone [1, 2]. Various pieces of evidence suggest that modern cultivars bred in favorable environments lack adequate adaptation to the

environment of A1 zone. Village surveys indicated that non-adoption of modern cultivars in western Rajasthan is due primarily to poor grain and stover yields under drought stress, which farmers expect 50% of the years [3]. This is supported by results of A1 zone research station trials in which modern varieties were found to be inferior to landrace materials in low yielding trials, and vice versa in higher yielding trials [4]. Comparisons of population crosses in both arid zone and more favorable environments indicated that only the arid zone landrace parents and landrace \times landrace populations were specifically adapted to the arid zone test environments [5]. Based on such observations, it has been suggested that breeding programs targeting the A1 zone require parental materials with specific adaptation to the arid-zone [6].

Various analyses of AICPMIP yield trials data have consistently indicated significant $G \times E$ interaction in AICPMIP trials [7], including the existence of crossover interactions [8]. AICPMIP trials however contain primarily open-pollinated varieties and hybrids from breeding programs targeting primarily grain yield in favorable environments. In addition, the $G \times E$ analyses done on these data sets have not attempted to analyze or cluster trial environments specifically by zone. The authors are unaware of any study done that specifically addresses the question of zone \times germplasm (cultivar type or origin) interactions. We recently conducted a two year study of genetic variation for ruminant nutritional quality in pearl millet, using a balanced set of arid zone landraces, dual-purpose open-pollinated varieties and grain-type F_1 hybrids, at representative A1, A and B zone locations [9]. This paper uses grain and biomass yield data from that study to assess evidence for cultivar type \times zone interactions, and their implications for the AICPMIP breeding program.

Materials and methods

Field trials: The experiment consisted of: (1) ten representative western or central Rajasthan landraces or landrace populations which had not in most cases

been improved by breeder selection, (2) ten improved, generally dual-purpose open-pollinated varieties, mainly from north Indian (including Rajasthan) breeding programs, and (3) ten publicly bred grain-type F₁ Hybrids, most of which either are or were widely grown by farmers, mainly in the A zone. The experiment was grown at Patancheru, Gwalior, Mandor and Nagaur (high and low input management) in 2000, and in Patancheru, Gwalior and Nagaur in 2001. Trials were completely rainfed, but otherwise managed for optimal growth and yield. Individual trials were grown in 4 (2000) or 6 (2001) row by 4.0 m plots in three replications. The center 2 (2000) or 4 (2001) rows of the plot were harvested and data recorded on field dry panicle, grain and stover weights, which were used to calculate total biomass, grain and stover yields on a square meter basis, and harvest index on a percent basis.

Data analysis: Trials were grouped by zone for purposes of analysis; the A zone was represented by Gwalior 2000 and 2001, the B zone by Patancheru 2000 and 2001, and A1 zone by the Mandor 2000 and Nagaur 2001. The two Nagaur trials in 2000 were subjected to very severe drought stress and were grouped separately to represent a severely stressed A1 zone environment, making a total of 4 zones/environments. Because of highly unequal variances

among zones and trials, data for each trial were normalized by converting individual plot values to standard deviation units above and below the mean for that trial, and the standardized data analyzed by the REML method with zone, cultivar type and their interaction as fixed effects and trial within zone, genotype within cultivar type and their interactions as random effects. Standardized cultivar type \times zone interaction means were plotted against zone to illustrate the relative adaptation of each cultivar type to each of the four zones.

Results and discussion

Zonal and cultivar type differences: Zonal differences in mean crop growth and yield were large, as expected. There was an almost four-fold range in total crop biomass among zones - from 240 g m⁻² in the A1 stress zone to 934 g m⁻² in the A zone (Table 1). Grain yields were lowest in the A1 (stress) zone, due to low values of both biomass and HI (a result of severe grain filling stress). Grain yields were approximately double in the A1 (normal) zone, due to both a greater biomass and a higher HI (Table 1). Grain yields were similar (and highest) in the A and B zones, as the higher biomass in the A zone was offset by a higher HI (an effect of the shorter daylength) in the B zone. The ranking of the stover yields generally

Table 1. Best linear unbiased estimators of cultivar type \times zonal means for biomass, harvest index and grain and stover yields in pearl millet. The first figures are the actual and figures in parentheses are the standardized means. SEDs for the comparison of standardized cultivar type means (within each zone), the zonal means (for each cultivar type), and for standardized cultivar type means across zones.

Zone/Cultivar type	Biomass (g m ⁻²)	HI (%)	Grain yield (g m ⁻²)	Stover yield (g m ⁻²)
A1 Zone (severe stress)	240	19.5	47.1	154.0
Dual-purpose OPV	215 (-.309)	16.7 (-.843)	35.8 (-.493)	146.0 (-.152)
Grain hybrid	237 (-.040)	23.5 (.644)	55.5 (.371)	139.0 (-.278)
Raj landrace	269 (.305)	18.5 (-.136)	49.8 (.132)	178.0 (.404)
A1 Zone (normal)	371	24.9	91.3	218.0
Dual-purpose OPV	379 (.080)	24.1 (-.137)	92.5 (.027)	226.0 (.136)
Grain hybrid	337 (-.304)	28.3 (.507)	94.6 (.097)	182.0 (-.474)
Raj landrace	398 (.216)	22.2 (-.382)	87.0 (-.131)	246.0 (.341)
A Zone	934	23.6	215.0	594.0
Dual-purpose OPV	1019 (.261)	24.2 (.091)	237.0 (.285)	650.0 (.183)
Grain hybrid	877 (-.206)	27.8 (.633)	240.0 (.389)	507.0 (-.430)
Raj landrace	906 (-.059)	18.9 (-.684)	169.0 (-.695)	624.0 (.236)
B Zone	570	37.5	217.0	282.0
Dual-purpose OPV	604 (.381)	38.0 (.033)	232.0 (.257)	298.0 (.318)
Grain hybrid	586 (.212)	43.1 (.902)	254.0 (.727)	255.0 (-.510)
Raj landrace	521 (-.580)	31.5 (-1.02)	165.0 (-.984)	294.0 (.214)
SED cultivar type (zone)	(.269)	(.238)	(.258)	(.292)
SED zone (cultivar type)	(.231)	(.186)	(.235)	(.236)
Across zones				
Dual-purpose OPV	554 (.103)	25.7 (-.124)	149.0 (.019)	330.0 (.121)
Grain hybrid	509 (-.085)	30.7 (.672)	161.0 (.396)	274.0 (-.423)
Raj landrace	523 (-.029)	22.8 (-.555)	118.0 (-.412)	335.0 (.299)
SED for cultivar type	(.179)	(.178)	(.159)	(.209)

followed the ranking of biomass, despite the differences among zones in HI; stover yields were highest in the A zone and lowest in the A1 (stress) zone (Table 1).

There were highly significant differences among the cultivar types for all four variables (Table 1). Across zones, the dual-purpose, open-pollinated cultivars and the arid zone landraces produced the greatest amount of biomass, and highest stover yields, and the grain-type F_1 hybrids had the highest HI and the greatest grain yield (Table 1). Cultivar type performance was highly dependent upon zone, however, as the cultivar type \times zone Wald statistics were highly significant ($P < 0.001$) for all variables except stover yield (data not presented). Genotype-within-cultivar type variances were generally similar (biomass and stover yield) or smaller than cultivar variances (HI and grain yield).

Cultivar type \times zone differences: The Rajasthan landraces produced the highest biomass and stover yields in both the A1 (stress) and A1 (normal) zones, and the second highest grain yield in the A1 (stress) zone (Table 1). However in the A and B less than that of the dual-purpose types (Table 1). The dual-purpose open-pollinated varieties, in contrast, produced the most biomass and stover in both the A and B zones, but were inferior to the landraces in the A1 (stress) zone and similar in the A1 (normal) zone. The grain yield of the dual-purpose types was lowest in the A1 (stress) zone, due to a very low HI, and was intermediate in the other three zones (Table 1). The grain-type F_1 hybrids were either the lowest or equal to the lowest biomass producers in all four zones, but maintained the highest harvest index across zones. As a result, they produced the highest grain yield, but the lowest stover yield, in all four zones (Table 1).

The nature of the cultivar type \times zone interactions was explored in more detail by plotting standardized values of all types for each zone (with zones arranged in equal intervals along the horizontal axis (Fig. 1). For biomass production, the Rajasthan landraces and dual-purpose open-pollinated varieties showed a strong crossover interaction, with the former producing the most biomass in the two A1 zones and the latter in the A and B zones (Fig. 1a). The grain-type F_1 hybrids were poor biomass producers in all three north India zones, but did relatively better in the B zone. For HI, the hybrids consistently had higher values in all zones, followed by the dual-purpose and Rajasthan landrace varieties (Fig. 1b). There was also an indication of a similar crossover interaction for HI as there was for biomass between the landrace and dual-purpose types, although it depended only upon the A1 (stress) zone in this case (Fig. 1b).

The pattern of interactions for grain yield generally

followed that for HI, with differing trends for all three cultivar types (compare Fig. 1c and 1b). However the superiority of the grain-type F_1 hybrids was less in the case of grain yield than in the case of HI, due to their generally inferior biomass production. The interactions for stover yield, in contrast, were a combination of the patterns for both biomass yield and for HI (Fig. 1d). The Rajasthan landraces had a relatively stable stover yield across zones, as relative partitioning to grain declined along with relative biomass in the A and B zones (Fig. 1a and 1b). In comparison, the pattern of stover yield of the dual-purpose open-pollinated cultivars followed the pattern of their biomass production, as their HI was less affected cultivars followed the pattern of their biomass production, as their HI was less affected by zone than was that of the Rajasthan landraces (Fig. 1a and 1b). The stover yield of the grain-type F_1 hybrids was also less affected by zone, as both their biomass yield and their HI were comparatively stable (Figs. 1d, 1a and 1b).

Basis of differential adaptation: The ability to produce biomass is a good basis of comparison for assessing adaptation to a specific environment, as it does not necessarily reflect past selection history, as does grain yield (unless selection has significantly affected crop duration). By this criterion, there was strong evidence of specific adaptation of the Rajasthan landraces to the A1 (stress) and A1 zones zone (Table 1; Fig. 1a). The superior ability of Rajasthan landraces to produce biomass in the A1 zone is not of itself surprising since these materials evolved under both natural and human selection in this environment. What is unexpected is that this adaptation to the arid zone environment seems to be at the cost of adaptation to the more favorable environments of the A and B zones. Although the absolute biomass production of the Rajasthan landraces increased as environment became more favorable (Table 1), it did so at a significantly lesser rate than did that of the dual-purpose open-pollinated varieties and grain-type F_1 hybrids, resulting in its standardized value becoming increasingly negative (Fig. 1a).

The dual-purpose cultivars, in contrast, exhibited an equally strong specific adaptation to the more favorable environments of the A and B zones (Fig. 1a). This cannot be explained simply as a history of selection of the dual purpose open-pollinated varieties in the A or B zones, as this group contains varieties bred in Rajasthan (A1 zone and drier part of the A zone) from both Rajasthan sources (RGB 2, WRajPop, RCB-IC 948) and non-Rajasthan sources (Raj 171, CZ-IC 923, RCB-IC 911) [10], as well as varieties bred in the A or B zones (Pusa 299, ICMV 155, WC-C75). However, the base populations or crosses from which the majority

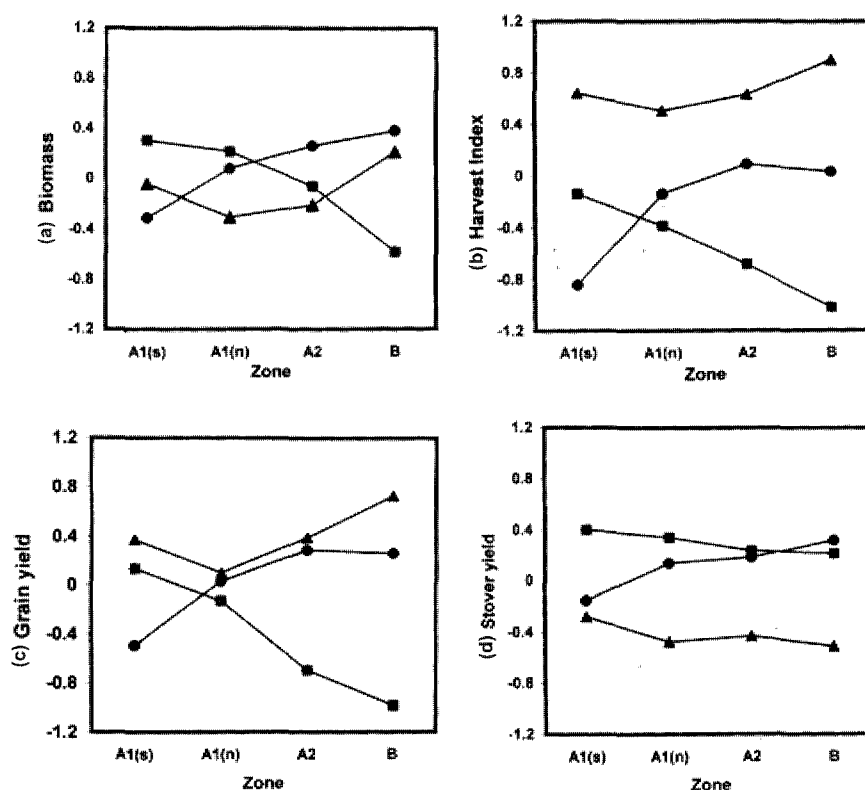


Fig. 1. Standardized cultivar type means for each of the four Indian millet-growing zones, for biomass (a), harvest index (b), grain yield (c) and stover yield (d). Cultivar types include Rajasthan landraces (squares), dual-purpose open-pollinated varieties (circles) and grain-type F₁ hybrids (triangles). Millet growing zone means are spaced equally along the x-axis in the following order: A1 (stress), A1 (normal), A and B, indicated as A1(s), A1(n), A, and B.

of the dual purpose varieties were bred are primarily adapted to the more favorable A and B zones, rather than to the A1 zone (with the exception of WRaj Pop and RCB 2). Thus it appears that the adaptation of the base populations from which these dual-purpose cultivars were selected is the most important determinant of adaptation, rather than the zone in which the selection was practiced. Presterl and Weltzien [5] reached a similar conclusion in their study of population crosses of mainly arid zone landrace \times elite breeding populations of non landrace origin, in which they reported a "clear loss of adaptation [to the arid zone] with these types of wide crosses."

The grain-type F₁ hybrids, in contrast to both the Rajasthan landraces and the dual-purpose open-pollinated varieties, did not exhibit specific adaptation to any particular environment, as judged by their standardized biomass (although this was relatively higher in the shorter daylength B zone than in either of the other three zones, Fig. 1a). The majority of the hybrids were bred in the A zone, although the seed parents used were bred in both the A and B zones. As released hybrids they would have been widely tested in AICPMIP trials and therefor would be expected to

have a reasonable adaptation to all zones, which this experiment confirms. Their relatively poor biomass production, however, indicates that while they do not show a specific zonal adaptation, their overall adaptation (by the definition used here) is poorer than that of the dual-purpose open-pollinated cultivar types (Table 1, Fig. 1a). This, however, is likely an artifact of their breeding history; as selection in this cultivar type is heavily biased towards grain yield and early maturity, with traditionally little emphasis on either biomass or stover yield.

Implications for breeding: No cultivar type demonstrated the optimal combination of a high level of biomass productivity with a non-specific zonal adaptation pattern, which suggests that the breeding of cultivars with adaptation to all three major pearl millet growing zones within India (by the definition of adaptation used in this paper) has not been achieved. Either the ability to produce biomass was specific to either the A1 or the more favorable zones, or else a broad adaptation in terms of grain yield was associated with relatively poor biomass productivity. Where the ability to produce stover is not a high priority, the current grain hybrids are clearly the best choice of

cultivar type, but where it is, current hybrids in general (although there may be individual exceptions) do not appear to have the ability to produce sufficient biomass to be fully acceptable to increase overall biomass production in the hybrids to increase in stover yield without a sacrifice of grain yield level [11], or else to exploit the specific zonal adaptation of the current open-pollinated types (landraces and dual-purpose cultivars) to breed varieties with good grain and stover yields for specific zones, rather than for all-India adaptation.

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